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THE STATUS OF *FONTARIA PULCHELLA* BOLLMAN,
WITH THE PROPOSAL OF A NEW GENUS AND TRIBE
IN THE DIPLOPOD FAMILY XYSTODESMIDAE*

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Millipeds of the genus *Nannaria* make up a characteristic and often very abundant element in the Appalachian-Ozarkian milliped fauna. So far about 20 forms have been named, and an even greater number of undescribed species are represented in my personal collection. Yet large areas of eastern North America have not been collected for these small, dominantly psychrophilous, xystodesmids, and I venture the prediction that as many as 200 species of *Nannaria* may eventually be accounted.

Although there is considerable variation in the gonopods among different species, the non-sexual characters—including coloration—tend to remain remarkably stable throughout the genus. Concomitantly, certain features of *Nannaria* collectively set the genus rather in apposition to most other xystodesmids, so that for many years I have thought that some suprageneric category might desirably be proposed as a means of signaling this disjunct position. Such inclinations have recently been crystallized by a sequence of events commencing with the receipt of a single male specimen from northern Georgia which, although closely related to *Nannaria*, represents a distinct and nameworthy branch of this group.

This specimen was at first taken to be of an undescribed species, and such may actually be its true status. However, a recent comparison with the two female cotypes of *Fontaria pulchella* at the U. S. National Museum shows that the male

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from Georgia agrees in every external detail with the long-enigmatic *pulchella* and is in all probability conspecific with the types. It must be remembered, however, that concordance in external features does not necessarily imply specific identity between millipeds, particularly of different sexes, so it is possible that topotypic males of *pulchella* will show gonopodal differences from the Georgia specimen. In the meantime, however, no great harm is done by the conservative treatment preferred here, and in the event of future emendation, it will merely be necessary to provide a new specific name based upon the Georgia milliped. There can be no doubt whatever, on the other hand, that the specimen is strictly congeneric with the types of *pulchella*, and differs enough from *Nannaria* to warrant separate status as a new genus. On the basis of this genus, and *Nannaria* (in the broad sense, to include "*Mimuloria*"), I venture to propose a new tribal category within the Xystodesmidae.

The occasion is also taken here to provide some illustrations of *Nannaria minor* Chamberlin, which, although the type species of its genus, has never been illustrated and which has thus remained an obstacle to a satisfactory understanding of *Nannaria* since its proposal in 1918.

I wish to thank my good friend and benefactor Leslie Hubricht for the gift of the male specimen here considered, and Dr. R. E. Crabill for access to the type material of *Fontaria pulchella* in the U. S. National Museum. The drawings are the work of my artist Anne Williams.

Family XYSTODESMIDAE Cook

Nannarini, new tribe

Components: *Nannaria* Chamberlin, 1918; *Oenomaea*, n. gen.

Diagnosis: Small, parallel-sided xystodesmids with the following characteristics: pretarsi of anterior legs of males (NOTE 1) broadened, spatulate, and usually strongly twisted; sterna of metazonites flat or but very slightly elevated medially, and produced into prominent subcoxal spines, the caudal edge of the metasterna is broadly convex and preceded by a flattened margin; anterior sterna of males narrow and unmodified except for two prominent paramedian knobs between the 4th pair of legs; gonopod aperture large, oval, extending laterad well beyond lateral ends of coxal sockets of the 7th segment; gonopods variable in form, usually elongate and slender, with acicular to laminate prefemoral process, the

coxae small and connected only by membrane, no sternal element persisting.

Range: Eastern North America from northern Georgia and Mississippi to New York, northern Illinois, Arkansas, and Missouri. Species are most abundant in the central Appalachian region, where almost any well-collected area will yield about four different species.

KEY TO THE GENERA OF NANNARINI

- Pretarsi of anterior legs of males simply flattened and spatulate, not strongly twisted at midlength (Fig. 4); posterior corner of paranota modified as a caudomedially projecting acumen on segments 3 through 16 (Fig. 1); solenomerite of male gonopods in the form of a broad, flat plate (Fig. 10) ----- *Oenomaea*, n. gen.
- Pretarsi of anterior legs of males flattened, distally spatulate, and strongly twisted at midlength (Fig. 6); posterior corners of paranota of most body segments rectangular or acutely angular, never projecting as a dentiform process (Fig. 5); solenomerite of gonopods variable but not in the form of a broad, flat plate *Nannaria* Chamberlin

Oenomaea, new genus

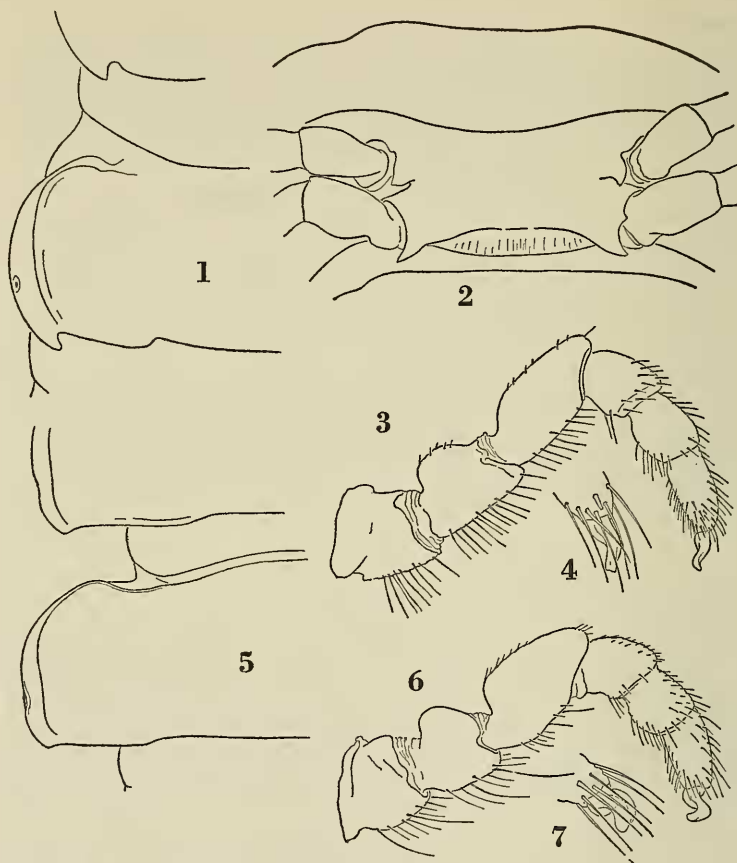
(Latinization of a classic Grecian proper name)

Type species: *Fontaria pulchella* Bollman, 1889.

Diagnosis: Differing from *Nannaria* by the characters stipulated in the preceding key. Head smooth and polished; epicranial suture distinct, ventrally bifurcate into two short, nearly horizontal interantennal sutures. Facial setae not yet determinable with assurance, but apparently as follows: epicranial 0-0, interantennal 1-1, subantennal 1-1, frontal 2-2, labral 14-14, genal 0-0. Genae nearly flat, without median impression, not margined laterally. Antennae unmodified, with four small terminal sensory cones.

Body relatively small in size, the width/length ratio about 15 per cent. Paranota small, depressed, especially on the anterior segments; anterior corners of paranota first rounded, then becoming obliquely sloped off on midbody and caudal segments; posterior corners of paranota of segments 4-16 acutely produced caudomesiad, the lateral edges convex (Fig. 1); posterior edges not margined. Ozopores in normal sequence, small, opening ventrolaterally in the caudal half of large, prominently thickened peritremata, their position gradually shifting more posteriorly on the caudal segments. Tergites smooth and polished, the metatergites slightly more convex than dorsum of prozonites, the two subsegments meeting dorsally at a fine, flat suture in a moderate interzonal stricture (NOTE 2).

Sterna smooth, nearly flat, sometimes transversely elevated between the posterior legpair, the elevated area then setting off a prominent broad, flat segmental marginal band (Fig. 2). No transverse or cruciform impressions; but sterna produced into conspicuous acutely pointed subcoxal spines. Sides of body unmodified. Stigmata similar in shape, elongate



FIGS. 1-4. *Oenomaea pulchella* (Bollman). 1, Left paranotum of 9th segment, dorsolateral aspect (perpendicular to paranotal surface); 2, Sternal areas and bases of legs of segment 10, ventral aspect; 3, 4th leg of male, anterior aspect; 4, End of tarsus and pretarsus of same, enlarged. FIGS. 5-7. *Nannaria minor* Chamberlin. 5, Left paranotum of 9th segment, dorsolateral aspect; 6, 4th leg of male, anterior aspect; 7, End of tarsus and pretarsus of same, enlarged.

vertical slits, the anterior stigmata somewhat larger than the posterior. Sternum of 5th segment produced into a prominent, median, apically notched process between the fourth pair of legs.

Coxae of legs mutic, prefemora with the usual long, sharp distal spines. Legs moderately long, the podomeres robust, densely setose ventrally; femoral segment the longest; pretarsi of anterior legs of males flattened,

spatulate; those of middle and posterior legs becoming slender and acute.

Gonopod aperture large, oval, extending far laterad and reducing the prozonite to a mere narrow transverse strip; edges of aperture moderately elevated on the caudal and lateral sides. Gonopods large, the coxae widely separated in situ, and connected only by membrane; coxae subglobose, with a few setae on the dorsal side but without coxal apophyses. Telopodites long and slender, projecting cephalad over the 6th sterna, curved medially and distally overlapping. An elongate, slender pre-femoral process is present; distally the telopodite is bifid into (1) an elongate, slender, tibial branch and (2) a much broader, laminate sole-nomerite (Fig. 10).

Female externally very similar to male, the sterna a little wider and the dorsum more convex. Cyphopodal characters not yet investigated.

Oenomaea pulchella (Bollman), new combination

(Figs. 1-4, 8-10)

Fontaria pulchella Bollman, 1889, Proc. U. S. Nat. Mus., 11: 316.

Nannaria pulchella Chamberlin and Hoffman, 1958, Bull. U. S. Nat. Mus., No. 212: 41.

Diagnosis: With the characters of the genus. This small species is readily distinguished from all other xystodesmids known to me by the peculiar formation of the paranota.

Type specimens: Two female cotypes, USNM (D-404), from Strawberry Plains, Jefferson Co., Tennessee, C. B. Branner, leg. I have designated the specimen in better condition as the *lectotype* of this species.

Description of male: (From wooded slope, 1.5 miles south of Oakman, Gordon Co., Georgia, 13 May 1961, Leslie Hubricht, leg.) Length about 26.5 mm, greatest width 4.8 mm; width/length ratio about 15 per cent. Body parallel-sided between segments 2 and 14, narrowing gradually caudal, width values for selected segments as follows:

Segment 1—4.2 mm	Segment 10—4.8 mm
2—4.7	12—4.8
4—4.8	14—4.7
6—4.8	16—4.3
8—4.8	18—4.0

Head capsule normal in appearance, oval, convex, smooth and polished, flattened between the antennae. Width across genae 2.9 mm. Epicranial suture thin but distinct, not in a depression, not punctate, but ventrally bifid, the branches horizontal and thus forming right angles with the main suture. Interantennal isthmus broad (1.0 mm), flat and smooth. Genae not margined laterally, and without evident median depression, the ends acutely rounded and projecting distinctly beyond adjacent margins of the cranium.

Facial setae partially abraded, the following data from apparent setae

sockets and thus subject to emendation: epicranial $\text{?}0-0$; interantennal 1-1; subantennal 1-1, each located near the lower, inner arc of the antennal socket; frontal 2-2, the outermost seta on each side more widely separated from the inner than the two inner setae are from each other; clypeal about 12-12; labral about 14-14; genal 0-0.

Antennae moderately long (4.9 mm) and slender, reaching back to middle of paranota of third segment. Article 1 globose, with a few apical setae; article 2 clavate, extending beyond genal apex; articles 2-6 similar in size and shape except that 2 is slightly more clavate than the others; articles 2-5 sparsely setose, 6 and 7 more densely setose, all with apical macrosetae; article 7 short, cylindrical, truncate, its distal edge not turned between the four small sensory cones, without sensory area on the outer surface.

Collum broad (about three times as broad as long), smooth and polished, elongate-hexagonal in shape, the anterior and posterior edges parallel, the posterior edge not emarginate middorsally; sides evenly converging laterad, the ends acutely rounded; a well-defined anterior marginal ridge.

Tergites of body segment entirely smooth and polished; paranota transverse, depressed, those of anterior segments continuing slope of dorsum, those farther back on body interrupting dorsal convexity. Peritremata thick and conspicuous, sharply set off from paranotal surface, scapuloae marginal on anterior segments, becoming submarginal farther back on body. Posterior edge of paranota thin, not margined. Prozonites and metazonites separated dorsally by a fine suture in a slightly constricted stricture, the metazonite slightly more convex and elevated.

Segments 2 and 3 similar in general appearance, the paranota transverse and depressed, with rounded anterior and posterior corners and moderately convex lateral edges. Segments 4-15 generally similar, the anterior corners of the paranota becoming gradually more rounded off and less convex, the scapuloae also becoming submarginal; posterior corners of these segments produced into acute, caudomedially directed spines formed by caudal prolongation of the peritremata. Posterior edge of these segments convex, forming a basal shoulder on the more caudal segments. Ozopores small, but distinct, opening on the ventrolateral side of the peritremata, their position gradually shifting caudally on successive segments until nearly at the base of the projecting dentation on segments 16-19.

Epipect large, subtriangular, slightly convex, smooth and polished, distinctly decurved distally, with the usual whorls of macrosetae. Paraplects nearly flat, smooth and glabrous with a few vertical striations, the medial edges very prominently elevated and sharply set off. Ventral seta set on a prominent discal tubercle located close to the marginal ridge; dorsal seta located in a small pit on the widest part of the ridge. Hypoplect large, transversely oval, with a faint median projection and prominent paramedian setiferous tubercles.

Sides of metatergites smooth and unmodified. Stricture very distinct

down sides, especially in front of paranota, as a broad but not sharply edged groove, but reduced to a shallow depression midventrally. Stigmata similar in shape, elongate oval, the edges not elevated above segmental surface, the anterior stigmata distinctly larger than the posterior; both are distinctly separated from the dorsal coxal condyles.

Sternal surfaces of metazonites smooth, glabrous, and nearly flat except for a very faint transverse elevation between the posterior pair of legs. Caudal edge of segment convex, flattened (Fig. 2). Both pairs of legs subtended by subcoxal spines, the anterior spines small and blunt, the posterior much larger, acute, curved caudolaterally, and projecting well beyond caudal edge of segment. Subcoxal spines each with 2 or 3 small setae. Anterior pair of legs slightly farther apart than the posterior. Sterna of anterior segments narrow and unmodified except for a robust, distally notched process between the 4th pair of legs. Sternum of 6th segment not depressed or broadened.

Legs relatively long and slender, the distal half of the femora visible from above when legs are extended laterad. Coxae unarmed, prefemora with long, sharp, distal spines, these two podomeres of approximately equal size. Length relationships of podomeres: $3 > 6 > 1 = 2 > 5 = 4$. See Figure 3 for appearance of 4th leg. First pair of legs reduced in size as usual, with acute pretarsi. Pretarsi of legs of 2nd-14th pairs distinctly broadened, flattened, and spatulate, but not twisted at midlength (Figs. 3 and 4).

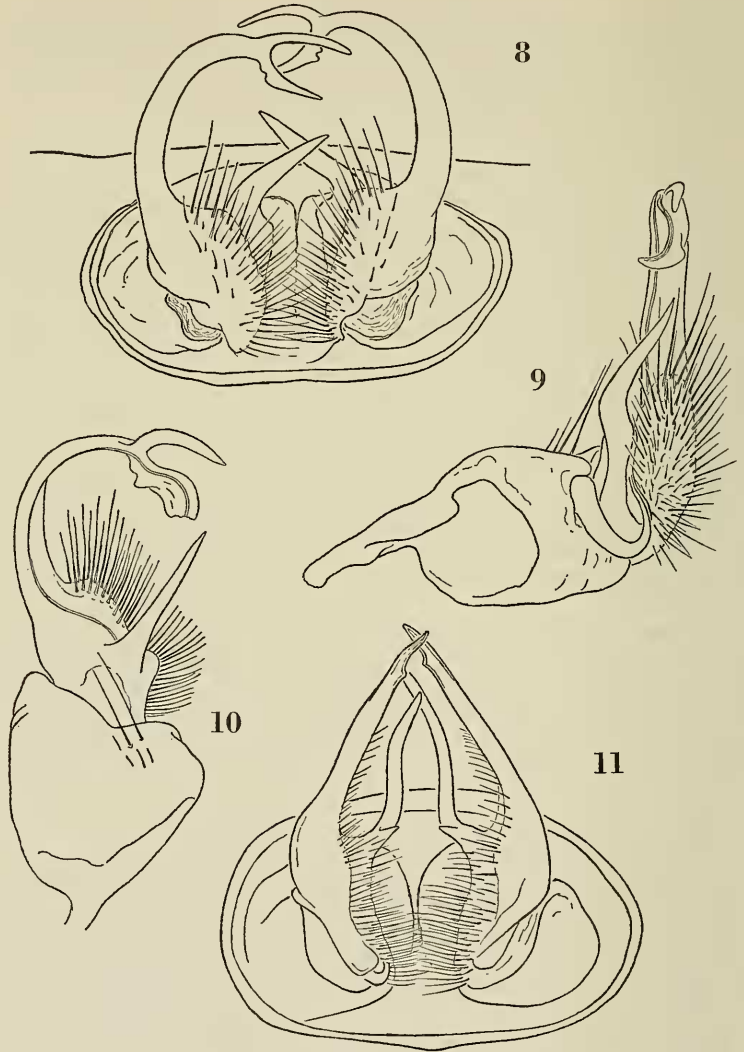
Prozonite of 7th segment reduced to a narrow, transverse strip by the large, symmetrically oval gonopod aperture, which extends laterally beyond ends of coxal sockets. Lateral and caudal edges slightly produced into a low marginal flange. Sternum behind gonopod aperture produced into two conspicuous, ventrally directed subcoxal cones. Gonopods large, of the form described in the generic diagnosis and shown in Figures 8-10.

Color in life unknown, the specimen apparently preserved shortly after moulting and at present testaceous-yellowish.

Remarks: Bollman's original description was extremely brief, but did mention most of the conspicuous features of this species. He correctly suspected a relationship with several species now referred to *Nannaria*, and described the coloration of his specimens as "Brown, lateral carinae and posterior border of segments red; legs and under parts yellow."

The recently published Checklist of North American millipeds (Chamberlin and Hoffman, 1958) refers *pulchella* to the genus *Nannaria*, without comment. It is a distinct pleasure to be able to finally dispose of this long-standing enigma and so reduce the number of dubious species of millipeds still on record for the eastern United States.

Both of Bollman's female types are smaller than the male specimen from Georgia, but the difference in size is no greater than the range of variation known for various other xystodesmids of similarly small size. The Georgia locality is about 115 miles south of Strawberry Plains, not an excessive distance for a specific range.



FIGS. 8-10. *Oenomaea pulchella* (Bollman). 8, Gonopods in situ, caudoventral aspect; 9, Left gonopod, mesial aspect; 10, Left gonopod, dorsal aspect. FIG. 11. *Nannaria minor* Chamberlin, gonopods in situ, caudoventral aspect.

Genus *Nannaria* Chamberlin(From the Latin *nannus*: small)*Nannaria* Chamberlin, 1918, *Psyche*, 25: 124.*Mimuloria* Chamberlin, 1928, *Ent. News*, 39: 155. NEW SYNONYMY!*Castanaria* Causey, 1950, *Chicago Acad. Sci. Nat. Hist. Misc.*, No. 73: 1.

Type species: Of *Nannaria*, *N. minor* Chamberlin, by original designation; of *Mimuloria*, *M. missouriensis* Chamberlin, by original designation; of *Castanaria*, *C. depalmai* Causey, by original designation.

Synonymy: *Mimuloria*, only recently recognized as a nannarine genus, has been distinguished by the small lamellate enlargement of the distal end of the gonopod telopodite. In the material at my disposal, including nearly 30 undescribed species, I find this character to be a mutable one, and more suitable for the distinction of a species-group than a separate genus.

Range: Eastern United States, chiefly in the Appalachian mountains, the Ozarks, and intervening states in the Central Lowlands.

Species: 21 have been described. Obviously a great number of species remain to be discovered.

Nannaria minor Chamberlin

(Figs. 5-7, 11)

Nannaria minor Chamberlin, 1918, *Psyche*, 25: 124.

Type specimen: Adult male (M.C.Z.), from Burbank, Carter Co., Tennessee; R. Thaxter, leg. I examined this specimen and drew the gonopods in February 1949.

Remarks: The original diagnosis of this species is reasonably adequate, but does not contain illustrations of the gonopods, and it is extremely difficult to formulate a good concept of such structures from a verbal description. It has never been possible heretofore to identify the species with confidence, and since my revision of *Nannaria* will not be completed for several years, I provide here some illustrations of the paranota, legs, and gonopods of *minor* for the benefit of other workers, as well as to provide a basis for comparison with the same characters in *Oenomaea*.

Nannaria minor has so far been known only from the type locality. The illustrated specimen is from a small series taken at a second locality: the southern side of Sam's Gap, along U. S. Hy. 23, in Madison Co., North Carolina, 23 July 1961, Hoffman, leg. This locality is 27 miles southwest of Burbank, and similarly in the Unaka Mountain range.

NOTES

NOTE 1. Pretarsi. The distalmost podomere (previously referred to as the tarsal claw by many workers) occurs in various forms among xystodesmid genera. So far I have distinguished three main types: one in which the pretarsus is only slightly curved, and is not evidently modi-

fied; a second in which it is elongate and bisinuate, with three or five distinct parallel carinae on the dorsal side; and a third in which the pretarsus is flattened, spatulate, and distally truncate (these distinctions refer to the condition on the anterior legs of the male sex). Insofar as North American genera are concerned, I find that these types correspond closely to generic groupings drawn along the lines of gonopods, metasterna, and other characters, and are therefore obviously useful in the discrimination of suprageneric categories. A more detailed treatment is contemplated following the examination of exotic members of the family.

NOTE 2. Stricture. The transverse constriction between prozonite and metazonite in polydesmoids, in which the segmental suture occurs, has been referred to in my earlier papers as the "interzonal furrow." This term is awkward and vernacular, and I am now glad to adopt the term "stricture" which was proposed by K. W. Verhoeff 30 years ago, although he failed to use it consistently in his later papers.

LITERATURE CITED

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